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Challenges and questions in reconstructing the ancestral flower of angiosperms: A reply to Sokoloff et al.

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Generations of botanists have developed hypotheses on the original angiosperm flower and patterns of early floral evolution. In recent years, several studies using a modern phylogenetic framework and large morphological data sets have contributed to a better understanding of trait combinations that might have characterized the flower of the most recent common ancestor of all living angiosperms (hereafter referred to as the ancestral flower) and its various modifications (Ronse De Craene et al., 2003; Zanis et al., 2003; Endress and Doyle, 2009; Doyle and Endress, 2011; Sauquet et al., 2017). In particular, the spatial organization of floral organs around a central axis, known as floral phyllotaxis, has fascinated botanists and mathematicians for a very long time (reviewed by Adler et al., 1997). Two basic types of floral phyllotaxis occur, whorled and spiral, although irregular patterns are also observed (Endress, 1987a; Endress and Doyle, 2007). Considerable effort has been made to reconstruct this key character in the ancestral flower, a question that has proven difficult to answer due to the particularly confounding variation among early-diverging lineages of angiosperms. Floral phyllotaxis therefore provides an excellent illustration of the challenges and problems one faces when reconstructing traits at the deepest nodes of the angiosperm phylogeny.

In our recent study based on a large data set of floral traits sampled from most families of angiosperms, we distinguished among perianth, androecium, and gynoecium phyllotaxis and reconstructed these three characters using both parsimony and model-based approaches (Sauquet et al., 2017). While our parsimony analyses were consistent with previous work in leaving these characters equivocal in the ancestral flower (Ronse De Craene et al., 2003; Zanis et al., 2003; Endress and Doyle, 2009; Doyle and Endress, 2011), our model-based results suggested the intriguing possibility that the ancestral flower might have possessed a whorled (trimerous) perianth and androecium, but a spiral gynoecium. Sokoloff et al. (2018) provided a very constructive criticism of this result, which they argued is unlikely given that this particular combination of character states has not been recognized in any living angiosperm flower. In doing so, Sokoloff et al. (2018) made many interesting and important points about our data set, analyses, and the interpretation of our results.

While we agree with some of the observations made by Sokoloff et al. (2018), we believe that some statements deserve further scrutiny and clarification. Briefly, (1) we argue that both developmental and anthetic data are important, but the lack of suitable developmental data in many species precludes their consistent use in scoring floral traits; (2) we acknowledge the few errors and alternative interpretations of the data highlighted by Sokoloff et al. (2018) and present updated analyses; (3) we question whether the absence of

a combination of character states among living taxa necessarily refutes its reconstruction in their ancestor; (4) we clarify why we decided to portray the ancestral flower with this combination, despite uncertainty and doubts among us; and (5) we raise the possibility that the ancestral flower was not necessarily whorled or spiral throughout and may instead have been polymorphic.

DEVELOPMENTAL VS. ANTHETIC DATA

Sokoloff et al. (2018) argued that our distinction between developmental and anthetic data is misleading and may have resulted in incorrect interpretations of particular taxa. While we address these specific examples in Appendix 1, several important general observations must be made. First, we certainly agree that careful developmental studies play a central role in understanding floral morphology and evolution. Not only do such studies document patterns of initiation and growth of floral organs during development, but they also often provide precise and reliable data on floral traits at anthesis. For the latter reason, we have used such studies as much as possible to score anthetic traits where they were available for the particular species of our sample. However, the lack of developmental data for most of the species of our sample made it impossible to score traits, including phyllotaxis, based on the full developmental sequence. To do so for only those well-studied species while scoring the rest based on their anthetic stage only would have resulted in an inconsistent and possibly biased data set. Alternatively, scoring phyllotaxis only in species for which good developmental studies are available would have resulted in an even greater proportion of missing data (with a possibly biased distribution), precluding any meaningful analyses of these characters.

In addition, important floral structural traits may differ between early developmental stages and anthesis. For instance, organs may be fused early on but appear to be free at anthesis (e.g., early sympetaly in Apiaceae; Erbar and Leins, 1996), actinomorphic flowers may be zygomorphic early in development and vice versa (Endress, 1999, 2012; Reyes et al., 2016), and organs present in early development may no longer be discernible at anthesis (e.g., the median stamen in many zygomorphic flowers of Lamiales; Borg and Schönenberger, 2011). Scoring species according to their early development when known, but according to their final anthetic stage when early developmental data are lacking would be problematic. It may also be misleading, depending on the goal of the analysis: for instance, from a functional point of view, the anthetic stage seems more important than the early developmental one. In the particular case of phyllotaxis, the situation is further complicated by common confusion between successive initiation and spiral phyllotaxis of organs (Endress, 2010): the former does not always imply the latter, which may only be verified by the divergence angles of successively initiated organs (Endress and Doyle, 2007; Staedler and Endress, 2009). Floral organs with spiral initiation may be slightly rearranged through development so that all divergence angles become equal at anthesis and thus form one or more whorls (e.g., Magnoliaceae and Ericales; Erbar and Leins, 1994; Schönenberger and Grenhagen, 2005; but see Appendix 1 for a discussion of the special case of *Illicium*). Such phenomena may or may not reflect the signature of an ancestral state, but even if they do, it would be problematic to refer to such data in ancestral state reconstruction analyses because the phylogenetic depth of such ancestry remains unknown.

Clearly, we would prefer to have high-quality developmental data at hand for all species included in our data set and we emphasize the need for continued research on floral development and morphology across angiosperms. However, even when such data become available, we argue that it will still be useful to distinguish between early development and anthesis, and we would advocate maintaining different characters rather than attempting to capture the full developmental sequence in one character.

THE CHALLENGES OF BUILDING A QUALITY DATA SET OF FLORAL TRAITS BASED ON PUBLISHED DATA

Sokoloff et al. (2018) pointed out some problematic data in our original study as they searched for unequivocal cases of "hemicyclic" flowers (sensu Sokoloff et al. [2018], i.e., with some organs arranged in a spiral but others in whorls) in angiosperms. Because these cases are not trivial, we discuss each problematic species in more detail in Appendix 1. Furthermore, we have updated our data set accordingly and present updated results, provided as Appendix S1 (data set) and Appendix S2 (results) in the Supplemental Data with this article. Clearly, we would all prefer a data set entirely built on solid, high-quality new observations made in a standard way across the entire sample of species included in our analyses. Although this is a desirable long-term target, it will require considerably more time and effort, and it was not an option for this first study. Thus, the problems highlighted by Sokoloff et al. (2018) serve as a good illustration of the challenges in building a quality data set entirely from published sources.

First, building very large data sets of traits, especially as a collaborative effort, inevitably entails occasional errors, regardless of the sources used. For instance, as pointed out by Sokoloff et al. (2018), we should have scored the flowers of *Peumus boldus* (Monimiaceae) as spiral throughout, as clearly shown in a detailed morphological study by two of us (Staedler and Endress, 2009). Despite our best efforts to check the data set, our erroneous (but now corrected) scoring of the gynoecium of this species as whorled had gone undetected, probably because of the unusual variation of Monimiaceae in floral phyllotaxis (Staedler and Endress, 2009). Therefore, we certainly appreciate the effort of Sokoloff et al. (2018) in scrutinizing our data set so carefully. We hereby encourage the community to share any other substantiated reports of potentially problematic data. Such cross-checking is important because it will help us to ensure continued improvement of both the quality and completeness of our data set, which we hope will be useful for several future studies of floral macroevolution. We also strongly encourage other colleagues who build morphological data sets to systematically provide the explicit source of every morphological record, as implemented in PROTEUS (Sauquet, 2016). This information (provided in Supplementary Data 13 of our original study; Sauquet et al., 2017) was clearly consulted by Sokoloff et al. (2018), allowing them to check and comment on the sources we used and enabling a fruitful and constructive discussion.

Second, as noted by Sokoloff et al. (2018), coding simple characters from the literature inevitably entails some difficult interpretations, even when the sources used appear to be ideal. We agree that some of our original scores of phyllotaxis in particularly difficult taxa (e.g., *Limeum* or Sabiaceae) are open to alternative interpretations. We have revised most of these records by deleting them (i.e., replacing them with missing data) rather than favoring one

of several controversial interpretations (Appendix 1). In doing so, we followed the general philosophy for our data set (i.e., missing data are more desirable than subjective data). However, we question whether "expert decision-making" (Sokoloff et al., 2018) is the best solution to these problems. While expert opinion is highly valuable, it may occasionally rely too much on hypothesis-driven interpretation rather than factual observation of structural data. As a result, expert interpretation may be biased among taxa and experts, representing a definite problem for building a large-scale, standardized data set such as ours.

The detailed investigation of Sokoloff et al. (2018) also underscores the many gaps left in our data set due to gaps in the literature. This is a somewhat frustrating consequence of our use of a strict exemplar approach to building this data set, but we propose that the future lies in careful morphological studies to fill in these gaps and in more densely sampled data sets rather than approximations made on the assumption that closely related species share the same floral traits. For this reason, we did not use *Hedycarya angustifolia* to inform the scoring of *Hedycarya arborea* (Appendix 1).

Sokoloff et al. (2018) noted that gynoecium phyllotaxis in our original data set was characterized by more missing data (49%) than for the perianth (11%) or the androecium (40%), which is partly due to the inapplicability of this character in unicarpellate gynoecia. They suggested that these differences in proportions of missing data might be responsible for our original inference of different phyllotaxis in the gynoecium vs. the perianth and androecium. To test this hypothesis, we analyzed a subset of our original data in which only the 293 taxa with all three characters scored and monomorphic were included and the remaining 499 taxa were scored entirely with missing data. Using exactly the same methods as in our original study (Sauquet et al., 2017), we found several differences in the analyses of the full data set (Appendix S2). Importantly, the reversible-jump Markov chain Monte Carlo (rjMCMC) analyses suggest an ancestral flower with spiral perianth, whorled androecium, and spiral gynoecium. Although this result should be interpreted with the greatest caution because of the comparatively small sample size, it demonstrates that the results of our original study cannot be simply attributed to differences in missing data among the three characters (analyses of our updated data set further prove this point, as proportions of missing data remained essentially the same: see results below). However, this experiment does suggest that taxon sampling is important for reconstructing such difficult characters with model-based approaches (there were no differences for parsimony in this experiment, partly because the early-diverging lineages remained well sampled in the subset analyses). Therefore, more confident answers may emerge from future analyses of better-sampled data sets, which will require much time and effort to assemble.

Our update of the data set following re-examination of the species highlighted by Sokoloff et al. (2018) includes changes in phyllotaxis characters for 10 species (in total 14 deleted records, 1 updated, 3 new). In addition, ongoing work on the data set since the published version of our study (Sauquet et al., 2017) has allowed us to fill gaps in phyllotaxis characters for 13 other species (in total 16 new records). In total, 34 data records were changed for the phyllotaxis characters (including 5 for the perianth, 16 for the androecium, and 13 for the gynoecium), affecting 23 species. Here, we report very briefly on the new results from analyses of this updated data set using exactly the same trees and methods as in our original study, focusing on the C tree series (Sauquet et al., 2017). We find no noticeable change for either perianth or androecium phyllotaxis, although we note increased support for an ancestral whorled perianth in the rjMCMC analyses (Appendix S2). However, the rjMCMC results of the new analyses suggest that gynoecium phyllotaxis was also ancestrally whorled rather than spiral in angiosperms, mesangiosperms, magnoliids, and eudicots, contrary to our original results for these nodes (ancestral gynoecium phyllotaxis did not change for the remaining key nodes). We also conducted again the same sensitivity experiment as in our original analyses, whereby we pruned out both core monocots and Pentapetalae to allow for a higher rate of phyllotaxis evolution in angiosperm lineages outside these two clades. We find very similar results to those based on our previous data set, whereby the ancestral flower is inferred to have been whorled throughout in both maximum likelihood and rjMCMC analyses, albeit with much uncertainty with the latter approach (Appendix S2).

While these new results are consistent with the view of Sokoloff et al. (2018) that the ancestral flower of angiosperms was probably either whorled or spiral throughout, we are not convinced by their argument that the absence or rarity of alternative arrangements among living angiosperms makes these alternatives far less plausible in the ancestral flower (see next section). Furthermore, our experience so far with the phyllotaxis characters suggests that it may be very difficult to reconstruct them with confidence at the base of the angiosperm tree. We predict that future analyses of this question based on subtle alterations of the data set or alternative approaches will produce inconsistent results, in contrast with the more stable and confident results we have obtained for other nodes and traits. Therefore, the new results presented here should be treated with the same caution as those from our initial study.

SHOULD WE DISMISS ANCESTRAL STATE COMBINATIONS NOT OBSERVED AMONG LIVING SPECIES?

Sokoloff et al. (2018) highlighted that no extant species sampled in our data set showed the combination of whorled perianth, whorled androecium, and spiral gynoecium that our analyses inferred as ancestral in angiosperms. Although we agree that our data set may provide a starting point for future quantitative analyses of floral traits in angiosperms, we believe it is still too small to be considered a "representative sample of overall floral diversity" and recommend caution in drawing statistics from it. However, the observations of Sokoloff et al. (2018) prompted us to look for examples of unsampled extant species showing the unusual combination of phyllotaxis characters, but likewise we could not find any. Despite the apparent absence of this combination in the modern flora, and despite the new results emerging from our updated data set (see above), we argue here that we should not dismiss ancestral state combinations that are no longer observed among extant species of a clade.

First, there may be a fundamental problem in rejecting morphologies no longer observed in extant species. The fossil record is full of examples of unusual forms that would be difficult to predict based only on extant species. For instance, the recently described flower of *Cecilanthus polymerus* from the Cenomanian of Maryland possesses at least 20 tepals, ca. 50 stamens (with possible H-valvate dehiscence), and ca. 100 plicate carpels, with probable whorled (or irregular) phyllotaxis throughout, a combination unknown in any living angiosperm (Herendeen et al., 2016). Phylogenetic analyses were in this case inconclusive, with multiple most-parsimonious positions in both early-diverging angiosperms and Magnoliidae.

Even if this fossil represents an apomorphic morphology in an extinct lineage, it seems undesirable to exclude de facto a hypothetical ancestral state reconstruction that inferred this combination of states as ancestral. Thus, although *Cecilanthus* does not address the special problem of differences in phyllotaxis within a flower, it does challenge the general argument that unobserved combinations are less likely to be ancestral.

Sokoloff et al. (2018) proposed that the absence of the combination of whorled perianth and androecium and spiral gynoecium among extant angiosperms implies the presence of a fundamental developmental constraint. We have varying views on the likelihood of such a constraint, but it is worth noting that several other types of constraint (architectural, ecological, historical) affect and may explain past, present, and future morphospaces (Chartier et al., 2014). An architectural constraint, whereby the combination we inferred as ancestral would be physically impossible, would provide the strongest argument against an unusual combination, but cannot be justified here. Likewise, an ecological (e.g., functional) constraint would be difficult to argue in this case (it may exist or have existed, but our knowledge is insufficient to articulate such a constraint). However, it is possible, in fact highly plausible, that the exact combination of character states that characterized the ancestral flower of all extant angiosperms no longer exists in nature, given the very long interval it has had to evolve (at least 140 million years), the great number of speciation events that occurred along most lineages, and the very profound changes in the environment that took place since that shared ancestor existed. Sokoloff et al. (2018) admit this point for the combination of all floral traits included in our analysis, but we do not see a clear rationale for why it would not apply to any combination of two particular traits.

From a methodological point of view, inferring ancestral state combinations is a more difficult endeavor. Current methods to test for correlated evolution and to infer ancestral states taking into account correlated evolution are still very limited for discrete characters and all rely on the original model of Pagel (1994), which uses a 4 by 4 Q matrix to represent all possible transitions among two co-evolving discrete characters. Because multivariate models for discrete character correlation are far too complex for inference, we decided to test and take into account correlated evolution by analyzing all possible pairwise combinations among floral traits in our original study (Sauquet et al., 2017). As noted by Sokoloff et al. (2018), we found a strong signal for correlated evolution among many pairs, including all three pairwise combinations among the three phyllotaxis characters. Taken individually, these analyses had suggested results only partly consistent with those of our separate single-trait analyses (see Supplementary Data 2 of our original study). For instance, when analyzing androecium and gynoecium phyllotaxis together, our rjMCMC analyses had suggested a spiral-whorled ancestor (the exact opposite of our reconstructed ancestral flower). However, this internal inconsistency might be attributed to the simplistic modeling of correlation between only two characters, while the real pattern might be much more complex and involve many more characters (including some not observed). In addition, while summarizing results across the entire suite of pairs tested, we actually found overall support for the results of single-trait analyses (for further details and discussion, see the section on these analyses in the Supplementary Discussion of our original study).

We advise great caution with the interpretation of such correlation analyses when state combinations are rare or absent among extant species. In such analyses, rare or absent state combinations implied by the model may drive the results in quite unpredictable ways because the data are not informative enough to estimate transitions to and from these combinations. As noted by Sokoloff et al. (2018), the spiral-whorled combination for the androecium and gynoecium phyllotaxis characters was very rare in our original data set, being recorded in only four species. Yet, when accounting for the significant correlation between androecium and gynoecium phyllotaxis, this rare combination was inferred as ancestral in angiosperms. We reanalyzed pairwise correlations among the three phyllotaxis characters in our updated data set and found slightly different but similarly inconsistent results (Appendix S2). These results arguably do not inspire confidence in current approaches to take correlation into account in ancestral state reconstruction, but they still illustrate that a combination absent from (or very rare among) extant members of a clade can technically be inferred as ancestral for this clade even when taking into account the strong correlation between two traits. Clearly, more methodological work is needed to characterize the conditions in which such results may be interpreted as an artifact.

THE RATIONALE BEHIND THE COMBINATION OF STATES PRESENTED IN OUR RECONSTRUCTED 3D MODEL

Sokoloff et al. (2018) asked why we decided to portray our reconstructed 3D model with the unusual combination of phyllotaxis states that we inferred from our analyses. In doing so, they raise an important point concerning the risks and benefits of choosing among multiple alternatives for the purpose of illustration when uncertainty remains for some characters. This point deserves further clarification on our part. Because our data set did not contain all possible floral features, our single 3D model inevitably contained some arbitrariness or subjectivity and should be seen as an example from a large number of possibilities. For instance, we did not reconstruct the size, shape, or color of floral organs, partly because these characters are too variable among closely related species and therefore evolve too fast to make an inference in deep time. Thus, our primary concern was that the model would accurately represent the results for those traits that were included in our analyses.

Various media outlets and colleagues have made unfortunate comparisons of our 3D model with flowers of the extant genus *Magnolia*, despite our best efforts to avoid any direct comparison with extant taxa. It is possible that the size, shape, and color of extant flowers inadvertently influenced the final rendering by the several artists involved in the project, but the comparison stops with these arbitrary features. We strongly encourage our botanical colleagues to avoid the temptation of taking our results as confirmation that the ancestral flower looked like that of *Magnolia*, which would be a return to the archetype favored by many botanists for much of the last century, beginning with Arber and Parkin (1907). First, our reconstructed flower differs significantly from that of Magnoliaceae in having stamens in whorls of three rather than a spiral. Second, most species of *Magnolia* have three trimerous whorls of tepals rather than at least four as portrayed in our model. Third, our figure shows perianth parts of similar size in all whorls, but it is equally likely that size increased from small in the outer (lower) tepals to larger in the inner (upper) ones. Such an increase is common in flowers with a multiparted perianth, whether the parts are whorled (Annonaceae, Berberidaceae) or spiral (*Illicium*, *Calycanthus*). Fourth, the decision to show the tepals as much larger than the stamens and carpels, as in *Magnolia*, was purely artistic; it is possible that they were not so much larger, as in *Amborella*

or *Trimenia*. Finally, although this character was not included in our study, parsimony analysis indicates that the carpels were ascidiate and not plicate as in *Magnolia* (Endress and Doyle, 2009).

Setting aside characters not included in our analyses, the persistent uncertainty in some characters that were reconstructed, such as phyllotaxis, implies that many different combinations are possible based on our results. It might have been desirable to portray at least some of these combinations, rather than one. However, this solution would have failed the primary purpose of the 3D model, which we offered primarily for science communication. To choose a single set of ancestral states without influence from prior theories on floral evolution, we opted for the state with the highest mean probability in our rjMCMC analyses. As suggested by our present updated analysis, it is likely that future analyses of larger, more densely sampled data sets, using more realistic models of evolution, will lead to different results, allowing us to refine the hypothetical portrait of the ancestral flower. Until then, we suggest that remaining as close as possible to our inferred estimates, without influence from other disciplines, such as developmental biology, was our best starting point to stimulate new discussions on floral evolution, where *a posteriori* input from other disciplines is of course desirable and essential.

NO STRONG EVIDENCE FOR AN ENTIRELY WHORLED OR ENTIRELY SPIRAL FLOWER

Our new analyses of an updated data set lend support to the view of Sokoloff et al. (2018) that the ancestral flower was either entirely whorled or entirely spiral. However, much uncertainty remains on the ancestral state of the three phyllotaxis characters at the base of the angiosperms, and the answer remains conditional on the approach or model used.

As revealed by the careful investigation of Sokoloff et al. (2018), "hemicyclic" flowers are rare among extant angiosperms, but they do exist. In addition, theoretical simulations provide a simple explanation for how hemicyclic flowers may develop in some circumstances, depending on the relative size of the floral organ primordia and floral apex (Douady and Couder, 1996; Jönsson et al., 2006). So why should we assume that the ancestral flower was not hemicyclic? It is possible that hemicyclic flowers represent transitional structures between entirely whorled and entirely spiral flowers, whereby a phyllotactic change occurred at one end of the floral axis, but had not reached the other end. If functional or developmental constraints favor entirely whorled or entirely spiral flowers, as Sokoloff et al. (2018) suggest, we would expect such transient states to be rare, but not necessarily absent, among both extant species and extinct ancestors. Thus, an intriguing possibility is that the ancestral flower was in the process of becoming entirely whorled or entirely spiral from an older ancestor (further down the stem lineage of angiosperms) that had the contrary phyllotaxis.

It is also possible that phyllotaxis in the ancestral flower was not fixed. First, it has long been recognized that many structural floral traits (including phyllotaxis) were probably more labile early in floral evolution than in more recent time periods and that this early lability has been retained by some members of early-diverging lineages of angiosperms, especially Magnoliidae (Endress, 1987a, b). Our preliminary tests by pruning core monocots and Pentapetalae have yielded estimates of rates of phyllotaxis evolution much higher than in angiosperms as a whole, consistent with this hypothesis. Second, polymorphic species for phyllotaxis have been documented. For instance, Doust (2000) showed that flowers of *Drimys winteri* could be either whorled or spiral, depending on events during development, including changes in meristem shape. Phyllotaxis may also be polymorphic in flowers of *Trochodendron aralioides* (Endress, 1990) and female flowers of *Hedycarya angustifolia* (Staedler and Endress, 2009), and we have observed whorled variants in typically spiral flowers such as *Austrobaileya scandens* and *Degeneria vitiensis* (H. Sauquet, unpublished data). However, the models used across our study assume constant rates of morphological evolution and do not explicitly allow multiple states to co-exist at the same time (polymorphic data are treated as uncertainty, not co-existence of two or more character states). Therefore, it is possible that future analyses allowing different rates in different parts of the phylogeny or during different time intervals, and/or using models that adequately allow for co-occurring states, will produce different results (including, perhaps, an ancestral flower with polymorphic phyllotaxis). From a general perspective, these questions represent an exciting area of ongoing work and a key challenge for studies of angiosperm macroevolution (Sauquet and Magallón, 2018).

Sokoloff et al. (2018) suggested that an alternative approach would be to treat floral phyllotaxis as a single character, scoring hemicyclic flowers as missing data. This approach would indeed simplify the question and would certainly prevent us from inferring a hemicyclic flower at any node of the phylogeny. While deciding on the final definitions of characters for the analyses in our original study, we made similar decisions for some rare states that fell outside of the core questions we were asking. For instance, we treated poricidal anther dehiscence, disymmetry, and hexamery as missing data in their respective characters, to avoid an inflation of the number of states and free parameters in the models we tested. Although such decisions often cannot be avoided, they come with the assumption that these rare states are probably terminal and apomorphic in the sample considered. Making this assumption for hemicyclic flowers would be risky. Furthermore, we disagree that this solution would provide a good opportunity to reduce the proportion of missing data in the character. If 49% of missing data remain for gynoecium phyllotaxis in our data set, it is in large part because the character is not applicable in many species (unicarpellate gynoecia) and the state could not be determined in many others. Treating all these gaps optimistically as the same character state as in the perianth (or androecium) would entail a level of assumption that would not help us move forward on the questions discussed here.

Sokoloff et al. (2018) further suggest that we should look into the fossil record for additional evidence to help us solve these difficult questions, citing three examples. We certainly agree that fossil evidence is essential, and we are currently developing our data set to allow future inferences that explicitly take into account fossil flowers. However, as we noted in our original study, the fossil record of flowers is still too young and too incomplete to provide any special support for ancestral floral traits: the oldest known flowers are already somewhat diverse and do not suggest any obvious new insights on the flower of the common ancestor (Sauquet et al., 2017). Many of the earliest known flowers are whorled and trimerous (Friis et al., 2011), but spiral flowers also exist in the Early Cretaceous (e.g., *Virginianthus calycanthoides*; Friis et al., 1994). Furthermore, most of these fossils have been attributed to stem lineages or crown groups of extant angiosperm clades (Doyle, 2015) and cannot inform us directly on the relative probability of floral traits in the common ancestor of all angiosperms estimated to have lived 140–250 million years ago (Magallón et al., 2015; Foster et al., 2017).

CONCLUSIONS

The critical discussion of our results by Sokoloff et al. (2018) is a valuable and necessary effort that has helped us improve our data set and reassess the plausibility of the ancestor portrayed in our original study (Sauquet et al., 2017). We hope that similar constructive comments will help us improve our understanding of early floral evolution. Importantly, this discussion has further highlighted the many gaps remaining in the published literature on floral morphology. Continued efforts to document floral structure and development through high-quality morphological studies will play an essential role in future refinement of our results. Here, we chose to focus on the most important points raised by Sokoloff et al. (2018) on our data and analyses. We deliberately did not address some of their intriguing suggestions concerning floral development, including 2.5 merism and bidirectional prepatterning. We are not convinced by these suggestions, but a discussion of them would be out of place here and will undoubtedly be addressed in future work by some of us and other colleagues.

Sokoloff et al. (2018) concluded that reconstructing ancestral states based on codified taxon–character matrices and mathematical algorithms (including both parsimony and model-based approaches) is a necessary but "reductionist" step toward understanding morphological evolution and advocated that results should always be interpreted in light of other evidence. We certainly agree with this general idea but, as we have argued here, we should be very cautious before dismissing results that might appear unusual or unexpected at first glance. The history of science is rich in discoveries that would have initially been dismissed based on common knowledge at the time. In angiosperm phylogenetics alone, the positions discovered through molecular analyses for *Amborella* (formerly considered a member of Monimiaceae, now the probable sister group of all remaining angiosperms) and Hydatellaceae (formerly placed in Poales, now the sister group of all remaining Nymphaeales) were initially surprising and unexpected. They stimulated considerable efforts to better characterize these taxa, and morphological features are now understood to corroborate their exclusion from the groups they had been placed in for decades.

We do not know yet with confidence whether the ancestral flower was entirely whorled, hemicyclic, or entirely spiral, because too much uncertainty remains on reconstruction of the phyllotaxis characters at the root of angiosperm phylogeny. More definitive answers to this question may come from analyses of more densely sampled data sets using more complex models (e.g., multivariate and rate-heterogeneous), explicit integration of fossil flowers into phylogenetic analyses, fossil discoveries closer to the age of the ancestral flower, and better understanding of phyllotaxis from a developmental genetic perspective. However, we hope that the agnostic results obtained from "reductionist statistics" of a large data set are stimulating a fresh new look at the evidence and are seriously challenging the old dogma of ancestral spiral phyllotaxis.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

LITERATURE CITED

Adler, I., D. Barabé, and R. V. Jean. 1997. A history of the study of phyllotaxis. *Annals of Botany* 80: 231–244.

Arber, E. A. N., and J. Parkin. 1907. On the origin of angiosperms. *Journal of the Linnean Society of London, Botany* 38: 29–80.

Borg, A. J., and J. Schönenberger. 2011. Comparative floral development and structure of the black mangrove genus *Avicennia* L. and related taxa in the Acanthaceae. *International Journal of Plant Sciences* 172: 330–344.

Brockington, S., P. Dos Santos, B. Glover, and L. R. De Craene. 2013. Androecial evolution in Caryophyllales in light of a paraphyletic Molluginaceae. *American Journal of Botany* 100: 1757–1778.

Chartier, M., F. Jabbour, S. Gerber, P. Mitteroecker, H. Sauquet, M. von Balthazar, Y. Staedler, et al. 2014. The floral morphospace – a modern comparative approach to study angiosperm evolution. *New Phytologist* 204: 841–853.

Douady, S., and Y. Couder. 1996. Phyllotaxis as a dynamical self organizing process part II: The spontaneous formation of a periodicity and the coexistence of spiral and whorled patterns. *Journal of Theoretical Biology* 178: 275–294.

Doust, A. N. 2000. The developmental basis of floral variation in *Drimys winteri* (Winteraceae). *International Journal of Plant Sciences* 162: 697–717.

Doyle, J. A. 2015. Recognising angiosperm clades in the Early Cretaceous fossil record. *Historical Biology* 27: 414–429.

Doyle, J. A., and P. K. Endress. 2011. Tracing the early evolutionary diversification of the angiosperm flower. *In* L. Wanntorp and L. P. Ronse De Craene [eds.], Flowers on the tree of life, 88–119. Cambridge University Press, Cambridge, UK.

Endress, P. K. 1987a. Floral phyllotaxis and floral evolution. *Botanische Jahrbücher für Systematik* 108: 417–438.

Endress, P. K. 1987b. The early evolution of the angiosperm flower. *Trends in Ecology & Evolution* 2: 300–304.

Endress, P. K. 1990. Patterns of floral construction in ontogeny and phylogeny. *Biological Journal of the Linnean Society* 39: 153–175.

Endress, P. K. 1995. Floral structure and evolution in Ranunculanae. *In* U. Jensen and J. W. Kadereit [eds.], Systematics and evolution of the Ranunculiflorae. Plant Systematics and Evolution, Supplement 9, 47–61. Springer, Vienna, Austria.

Endress, P. K. 1999. Symmetry in flowers: Diversity and evolution. *International Journal of Plant Sciences* 160: S3–S23.

Endress, P. K. 2001. The flowers in extant basal angiosperms and inferences on ancestral flowers. *International Journal of Plant Sciences* 162: 1111–1140.

Endress, P. K. 2010. Flower structure and trends of evolution in eudicots and their major subclades. *Annals of the Missouri Botanical Garden* 97: 541–583.

Endress, P. K. 2012. The immense diversity of floral monosymmetry and asymmetry across angiosperms. *Botanical Review* 78: 345–397.

Endress, P. K., and J. E. Armstrong. 2011. Floral development and floral phyllotaxis in *Anaxagorea* (Annonaceae). *Annals of Botany* 108: 835–845.

Endress, P. K., and J. A. Doyle. 2007. Floral phyllotaxis in basal angiosperms: development and evolution. *Current Opinion in Plant Biology* 10: 52–57.

Endress, P. K., and J. A. Doyle. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. *American Journal of Botany* 96: 22–66.

Erbar, C., and P. Leins. 1994. Flowers in Magnoliidae and the origin of flowers in other subclasses of the angiosperms. I. The relationships between flowers of Magnoliidae and Alismatidae. *In* P. K. Endress and E. M. Friis [eds.], Early evolution of flowers. Plant Systematics and Evolution Supplement 8, vol. 8, 193–208. Springer, Vienna, Austria.

Erbar, C., and P. Leins. 1996. Distribution of the character states "early sympetaly" and "late sympetaly" within the "Sympetalae Tetracyclicae" and presumably allied groups. *Botanica Acta* 109: 427–440.

Foster, C. S. P., H. Sauquet, M. van der Merwe, H. McPherson, M. Rossetto, and S. Y. W. Ho. 2017. Evaluating the impact of genomic data and priors on Bayesian

estimates of the angiosperm evolutionary timescale. *Systematic Biology* 66: 338–351.
Friis, E. M., P. R. Crane, and K. R. Pedersen. 2011. Early flowers and angiosperm evolution. Cambridge University Press, Cambridge, UK.
Friis, E. M., H. Eklund, K. R. Pedersen, and P. R. Crane. 1994. *Virginianthus calycanthoides* gen. et sp. nov.—A calycanthaceous flower from the Potomac Group (Early Cretaceous) of eastern North America. *International Journal of Plant Sciences* 155: 772–785.
Hayes, V., E. L. Schneider, and S. Carlquist. 2000. Floral development of *Nelumbo nucifera* (Nelumbonaceae). *International Journal of Plant Sciences* 161: S183–S191.
Herendeen, P. S., J. A. Doyle, P. K. Endress, and M. Takahashi. 2016. *Cecilanthus polymerus*, a novel multiparted flower from the mid-Cretaceous Rocky Point locality, Maryland. *Botany* 94: 787–803.
Hirmer, M. 1931. Zur Kenntnis der Schraubenstellungen im Pflanzenreich [On spiral phyllotaxis in the plant kingdom]. *Planta* 14: 132–206.
Jönsson, H., M. G. Heisler, B. E. Shapiro, E. M. Meyerowitz, and E. Mjolsness. 2006. An auxin-driven polarized transport model for phyllotaxis. *Proceedings of the National Academy of Sciences, USA* 103: 1633–1638.
Leandri, J. 1958. Famille Euphorbiaceae, tome 1. Flore de Madagascar et des Comores (plantes vasculaires), famille 111, 1–199. Firmin-Didot, Paris, France.
Magallón, S., S. Gómez-Acevedo, L. L. Sánchez-Reyes, and T. Hernández-Hernández. 2015. A metacalibrated time-tree documents the early rise of flowering plant phylogenetic diversity. *New Phytologist* 207: 437–453.
Pagel, M. 1994. Detecting correlated evolution on phylogenies: A general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society, B, Biological Sciences* 255: 37–45.
Reyes, E., H. Sauquet, and S. Nadot. 2016. Perianth symmetry changed at least 199 times in angiosperm evolution. *Taxon* 65: 945–964.
Ronse De Craene, L. P. 2004. Floral development of *Berberidopsis corallina*: a crucial link in the evolution of flowers in the core eudicots. *Annals of Botany* 94: 741–751.
Ronse De Craene, L. P. 2010. Floral diagrams: an aid to understanding flower morphology and evolution. Cambridge University Press, Cambridge, UK.
Ronse De Craene, L. P. 2013. Reevaluation of the perianth and androecium in Caryophyllales: implications for flower evolution. *Plant Systematics and Evolution* 299: 1599–1636.
Ronse De Craene, L. P. 2017. Floral development of *Berberidopsis beckleri* – Can an additional species of the Berberidopsidaceae add evidence to floral evolution in the core eudicots? *Annals of Botany* 119: 599–610.
Ronse De Craene, L. P., D. Quandt, and L. Wanntorp. 2015. Floral development of *Sabia* (Sabiaceae): Evidence for the derivation of pentamery from a trimerous ancestry. *American Journal of Botany* 102: 336–349.
Ronse De Craene, L. P., P. S. Soltis, and D. E. Soltis. 2003. Evolution of floral structures in basal angiosperms. *International Journal of Plant Sciences* 164: S329–S363.
Sampson, F. B. 1969. Studies on the Monimiaceae. I. Floral morphology and gametophyte development of *Hedycarya arborea* J.R. et.G. Forst. (subfamily Monimioideae). *Australian Journal of Botany* 17: 403–424.
Sattler, R. 1973. Organogenesis of flowers: a photographic text atlas. University of Toronto Press, Toronto, Ontario, Canada.
Sauquet, H. 2016. PROTEUS: A database for recording morphological data and creating NEXUS matrices, version 1.26. Website http://eflower.myspecies.info/proteus.
Sauquet, H., M. von Balthazar, S. Magallón, J. A. Doyle, P. K. Endress, E. J. Bailes, E. Barroso de Morais, et al. 2017. The ancestral flower of angiosperms and its early diversification. *Nature Communications* 8: 16047.
Sauquet, H., and S. Magallón. 2018. Key questions and challenges in angiosperm macroevolution. *New Phytologist*: in press.
Schönenberger, J., and A. Grenhagen. 2005. Early floral development and androecium organization in Fouquieriaceae (Ericales). *Plant Systematics and Evolution* 254: 233–249.
Sokoloff, D. D., M. V. Remizowa, R. M. Bateman, and P. J. Rudall. 2018. Was the ancestral angiosperm flower whorled throughout? *American Journal of Botany* 105: 5–15.
Spongberg, S. A. 1976. Magnoliaceae hardy in temperate North America. *Journal of the Arnold Arboretum* 57: 250–312.
Staedler, Y. M., and P. K. Endress. 2009. Diversity and lability of floral phyllotaxis in the pluricarpellate families of core Laurales (Gomortegaceae, Atherospermataceae, Siparunaceae, Monimiaceae). *International Journal of Plant Sciences* 170: 522–550.
Wanntorp, L., and L. P. Ronse De Craene. 2007. Flower development of *Meliosma* (Sabiaceae): evidence for multiple origins of pentamery in the eudicots. *American Journal of Botany* 94: 1828–1836.
Williams, E. G., T. L. Sage, and L. B. Thien. 1993. Functional syncarpy by intercarpellary growth of pollen tubes in a primitive apocarpous angiosperm, *Illicium floridanum* (Illiciaceae). *American Journal of Botany* 80: 137–142.
Wróblewska, M., A. Dołzbłasz, and B. Zagórska-Marek. 2016. The role of ABC genes in shaping perianth phenotype in the basal angiosperm *Magnolia*. *Plant Biology* 18: 230–238.
Xu, F., and P. J. Rudall. 2006. Comparative floral anatomy and ontogeny in Magnoliaceae. *Plant Systematics and Evolution* 258: 1–15.
Zanis, M. J., P. S. Soltis, Y. L. Qiu, E. Zimmer, and D. E. Soltis. 2003. Phylogenetic analyses and perianth evolution in basal angiosperms. *Annals of the Missouri Botanical Garden* 90: 129–150.
Zhang, X., and Y. Ren. 2008. Floral morphology and development in *Sargentodoxa* (Lardizabalaceae). *International Journal of Plant Sciences* 169: 1148–1158.

APPENDIX 1. NOTES ON SPECIFIC TAXA.

Androstachys johnsonii (Picrodendraceae, Malpighiales)

We agree with Sokoloff et al. (2018) that current data are insufficient for a confident interpretation of androecium phyllotaxis in this species. However, until proven otherwise, we maintain our original record of spiral phyllotaxis, which was based on the treatment of Euphorbiaceae in the Flore de Madagascar (Leandri, 1958). We agree with Sokoloff et al. (2018) that this species may represent one of several examples of unisexual flowers with whorled female flowers and spiral male flowers, which are not uncommon among apetalous taxa (Endress, 1987a).

Berberidopsis corallina (Berberidopsidaceae, Berberidopsidales)

As highlighted by Sokoloff et al. (2018), androecium phyllotaxis in this species is unclear, although we agree that current data might suggest an interpretation as whorled (Ronse De Craene, 2004, 2010, 2017). The androecium phyllotaxis of this species has been left as missing data in our data set.

Chenopodium album (Amaranthaceae, Caryophyllales)

This species was not included in our data set. However, we disagree with Sokoloff et al. (2018) that it is relevant in the discussion on ancestral phyllotaxis. According to the diagram given by Sattler (1973), the phyllotaxis is whorled. The only unusual trait is that there is no alternation between the sepals and stamens, as is often the case in apetalous Caryophyllales and other eudicots. Unfortunately, the light micrographs of Sattler (1973) are so unclear that details of development cannot be recognized. In addition, the argument that interpretation of phyllotaxis is dependent on outgroup comparison is not valid for our data set, where we explicitly avoided this type of scoring (although we acknowledge that such a rationale may be useful in other contexts).

***Forstera bidwillii* (Stylidiaceae, Asterales)**

We agree with Sokoloff et al. (2018) that the androecium of this species should not have been scored as spiral and have deleted our original record, which was an error. Furthermore, we agree that scoring phyllotaxis for organ sets comprising only two parts can be problematic, especially when zygomorphy is involved as is the case for this species. However, for this data set, we cannot accept the argument that the androecium was originally pentamerous in the family as a rationale for scoring. Thus, androecium phyllotaxis of this species is now treated as missing data in our updated data set.

***Hedycarya arborea* (Monimiaceae, Laurales)**

Floral phyllotaxis in Monimiaceae is particularly variable and the fact that the androecium of *Hedycarya angustifolia* has been shown to be whorled (Staedler and Endress, 2009) certainly does not imply that the androecium of *Hedycarya arborea* is also necessarily whorled. In addition, phyllotaxis was actually found to be polymorphic in female flowers of *Hedycarya angustifolia*, depending on organ number (Staedler and Endress, 2009). However, we agree with Sokoloff et al. (2018) that the observations of Sampson (1969) are insufficient to document androecium phyllotaxis in *Hedycarya arborea* and have now deleted this record. Thus, androecium phyllotaxis of this species is now treated as missing data in our updated data set.

***Illicium floridanum* (Schisandraceae, Austrobaileyales)**

Sokoloff et al. (2018) mentioned the difficulty posed by the special case of floral phyllotaxis in *Illicium*, stating that its gynoecium is spiral in young stages and whorled in mature flowers. This statement is not correct. Apparently, they only inspected scanning electron micrographs of advanced flowers seen from above. However, for thorough study of floral phyllotaxis, it is necessary to consider the organs at the attachment level, and in *Illicium* this level cannot be seen in such micrographs because it is hidden below the upper parts of the organs. In addition, in *Illicium* the attachment level of the organs is not horizontally flat but has the shape of a steep cone. Nevertheless, it can be seen on such images (e.g., Endress, 2001: fig. 7H) that the innermost edges of the carpels, which of all visible floral parts are those closest to the organ attachment level, have different distances from the midpoint of the flower and also slightly different shapes. The flowers of *Illicium* have another special feature that makes phyllotaxis determination somewhat tricky. After the formation of all floral organs, the remaining floral apex is transformed into a massive dome, which functions at anthesis as an unusual kind of extragynoecial compitum (Williams et al., 1993). The breadth of this dome has the effect that the four rings of floral organs, which are already formed, take up more circumferential space, and their distance from the floral center becomes unusually large. However, the angular (radial) distance of successively initiated organs, and thus the divergence angles, do not change. But this configuration has the effect that in later stages the relative distance differences to the floral center become minimized and almost disappear on superficial inspection (e.g., see Hirmer 1931). As a rule, phyllotaxis determination is possible neither in too early stages when not yet all floral organs are present (or at least when not yet all sectors of the young flowers are occupied by floral organs), nor in too old stages, when further growth may transform the flower (e.g., from polysymmetry to monosymmetry or asymmetry, which is, however, not the case here). In our original data set, we acknowledged these problems by scoring gynoecium phyllotaxis as ambiguous (whorled / spiral) for this species. Although we believe the line of evidence discussed here suggests that gynoecium phyllotaxis of *Illicium* remains spiral at anthesis, scoring it as such would set the standard too high for the rest of our data set. Therefore, we maintain our scoring of gynoecium phyllotaxis for this species as ambiguous (effectively treated as missing data in our analyses).

***Limeum africanum* (Limeaceae, Caryophyllales)**

The unusual floral structure and development of this species made it particularly difficult to score for androecium phyllotaxis, despite the availability of the detailed study by Brockington et al. (2013). We agree with Sokoloff et al. (2018) that our original interpretation of a spiral androecium based on these data is questionable and that an interpretation as whorled is also possible. However, the argument that the androecium of Caryophyllales is basically whorled (Ronse De Craene, 2013) cannot be used for this study, where we explicitly avoided scoring species based on presumed ancestral states of their clade. Therefore, we have now deleted this record and androecium phyllotaxis of this species is now treated as missing data in our updated data set.

Magnoliaceae (Magnoliales)

Although detailed morphological studies are rare for this family, most species of Magnoliaceae indeed appear to have a whorled perianth, a spiral androecium, and a spiral gynoecium (Erbar and Leins, 1994; Xu and Rudall, 2006; Wróblewska et al., 2016). Less commonly, the perianth appears to combine both traditional trimerous whorls and additional, spirally arranged inner parts interpreted to represent petaloid staminodes, as in *Magnolia stellata* (Wróblewska et al., 2016). Therefore, most Magnoliaceae should indeed represent typical examples of cyclospiral flowers sensu Sokoloff et al. (2018). Although we should remain cautious about reports of spiral phyllotaxis in the taxonomic literature (Endress and Armstrong, 2011) and had difficulties finding suitable data for *Magnolia tripetala* (the species of the genus sampled in our data set), there is little doubt that the description of this and other North American species as having a spiral androecium is correct (Spongberg, 1976). In our original data set, the androecium of *Liriodendron chinense* was scored as spiral, but that of *Magnolia tripetala* was left unscored. The androecium phyllotaxis of both species is now scored as spiral in our updated data set.

***Nelumbo lutea* (Nelumbonaceae, Proteales)**

Upon closer examination, we agree with Sokoloff et al. (2018) that androecium phyllotaxis in this species is difficult to determine and could be irregular, rather than whorled as originally scored in our data set (Hayes et al., 2000). Therefore, we have now deleted this record, and androecium phyllotaxis of this species is now treated as missing data in our updated data set.

***Peumus boldus* (Monimiaceae, Laurales)**

As noted by Sokoloff et al. (2018), the flowers of this species are clearly spiral throughout (Staedler and Endress, 2009), and our

scoring of the gynoecium as whorled was an error, which we have now corrected. Thus, gynoecium phyllotaxis of this species is now scored as spiral in our updated data set.

Sabiaceae (Proteales)

We agree with Sokoloff et al. (2018) that interpretation of floral phyllotaxis in Sabiaceae is particularly challenging. Although Wanntorp and Ronse De Craene (2007) originally interpreted the flowers of *Meliosma* as spiral throughout (an interpretation followed in our original scoring of *Meliosma veitchiorum*), Endress (2010) and later Ronse De Craene et al. (2015) proposed that all flowers of Sabiaceae are instead essentially whorled, with alternation of trimerous and dimerous whorls, leading to the impression of pentamerous whorls. We note that this interpretation is consistent with our reconstruction of the ancestral flower of eudicots as whorled (Sauquet et al., 2017), but we certainly cannot use this rationale for scoring species in our data set. Importantly, we reject the argument of Sokoloff et al. (2018) that floral phyllotaxis should be scored uniformly in *Sabia* and *Meliosma*, given that floral structure of these two genera is not identical, and we must point out that in this case expert opinion on the interpretation of these flowers has changed through time (Wanntorp and Ronse De Craene, 2007; Ronse De Craene et al., 2015). However, in light of this discussion, we have now decided that it would be safer to choose neither interpretation and therefore deleted all our original records of phyllotaxis for the two species of Sabiaceae sampled in our data set. Thus, floral phyllotaxis of both species of Sabiaceae is now treated as missing data for the three characters (perianth, androecium, gynoecium) in our updated data set.

***Sargentodoxa cuneata* (Lardizabalaceae, Ranunculales)**

We agree with Sokoloff et al. (2018) that the observations of Zhang and Ren (2008) provide good evidence that androecium and gynoecium phyllotaxis in this species is whorled (or irregular), and not spiral, contrary to the scoring of the gynoecium in our original data set based on another source (the androecium had been left unscored). We have now corrected the scoring. As a result, both androecium and gynoecium phyllotaxis for this species is now scored as whorled in our updated data set.

***Xanthorhiza simplicissima* (Ranunculaceae, Ranunculales)**

The photograph of an anthetic flower of this species by Endress (1995: fig. 7C) clearly suggests spiral phyllotaxis, but it is possible that this species is polymorphic. In the absence of more detailed observations, we think it is safer to treat phyllotaxis of all organs as unknown and have now deleted our original records of perianth and androecium phyllotaxis for this species. Thus, floral phyllotaxis is now treated as missing data for the three characters (perianth, androecium, gynoecium) for this species in our updated data set.